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Phylogenetic Implications of the Spur Structures of the Hind Tibia in the Formicidae (Hymenoptera)

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Abstract The structures of the spur on the hind tibia in the family Formicidae were investigated by SEM. Plesiomorphic conditions were found in the spur morphology and articulation to the tibia of Formicinae, whereas different apomorphic conditions were found in the other subfamilies examined. This supported the notion that the Formicinae is a very early derived group in the formicid evolution.

Key words: Phylogeny; hind-tibial spur; Formicidae; Hymenoptera; SEM.

Introduction

Formicidae is currently divided into ten existing subfamilies: Myrmeciinae, Pseudomyrmecinae, Formicinae, Dolichoderinae, Aneuretinae, Dorylinae, Leptanillinae, Cerapachyinae, Ponerinae and Myrmicinae, and one extinct subfamily: Sphecomyrminae (WHEELER & WHEELER, 1972).

Despite several excellent works on the phylogeny of Formicidae, a relationship of these subfamilies remains uncertain (*e.g.*, WHEELER, 1928; BROWN & NUTTING, 1950; BROWN, 1954; GOTWALD, 1969; TAYLOR, 1978, etc.). Phylogenetic analysis of organisms is essentially based on the information contained in their characters (WILEY, 1981). A more accurate understanding of the formicid phylogeny still requires more knowledge on their characters.

BROTHERS (1975), analyzing the phylogeny of Aculeata at family level, illustrated that Formicidae had expanded hind-tibial spur with a row of teeth, which is considered as one of the unique apomorphic (derived) condition for the family Formicidae. The formicids are, however, expected to have other apomorphic characters in the spur morphology than BROTHERS (1975) indicated, since materials he surveyed were very limited.

The present study intended to more extensively survey the structures of hind-tibial spur in Formicidae to discuss the phylogenetic implications.

Materials and Methods

Taxa examined. The species examined were listed in Table 1. In the following observations, worker specimens were investigated, because it is by far the best known and most available caste.

Table 1. List of taxa examined.

Formicinae: *Acropyga baodaoensis* TERAYAMA, *Anoplolepis longipes* (JERDON), *Camponotus haberei* FOREL, *C. japonicus* MAYR, *Colobopis nipponicus* WHEELER, *Echinopla* sp., *Formica fukaii* WHEELER, *F. japonica* MOTSCHULSKY, *Lasius flavus* (FABRICIUS), *L. niger* (LINNAEUS), *Melophorous* sp., *Oecophylla samaragdina* FABRICIUS, *Paratrechina bourbonica* (FOREL), *Plagiolepis* sp., *Polyergus samurai* YANO, *Polyrhachis dives* F. SMITH, *Prenolepis* sp., *Prolasius* sp.
Dolichoderinae: *Bothriomyrmex* sp., *Dolichoderus bituberculatus* MAYR, *Iridomyrmex itoi* FOREL, *Tapinoma indicum* FOREL, *Technomyrmex gibbosus* (WHEELER).
Myrmeciinae: *Myrmecia gulosa* (FABRICIUS), *M.* sp.
Pseudomyrmecinae: *Tetraponera allaborans* WALKER, *T.* sp.
Dorylinae: *Aenictus laeviceps* (F. SMITH), *A. lifuiae* TERAYAMA, *Dorylus* sp.
Leptanillinae: *Leptanilla japonica* BARONI URBANI.
Cerapachyinae: *Cerapachys biroi* FOREL, *C. sauteri* FOREL.
Myrmicinae: *Aphaenogaster famelica* (F. SMITH), *Cardiocondyla nuda* (MAYR), *Cataulacus* sp., *Crematogaster matsumurai* FOREL, *Epitritus hexamerus* BROWN, *Kyidris mutica* BROWN, *Messor aciculatus* (Fr. SMITH), *Myrmecina graminicola nipponica* WHEELER, *Myrmica jessensis* FOREL, *Oligomyrmex sauteri* FOREL, *Pentastruma canina* BROWN et BOISVERT, *Pheidole pieli* SANTSCHI, *Pheidogeton* sp., *Pristomyrmex pungenus* MAYR, *Smithistruma japonica* (ITO), *Solenopsis* sp., *Strumigenys lewisi* CAMERON, *Tetramorium caespitum* (LINNAEUS), *Vollenhovia emeryi* WHEELER.
Ponerinae: Amblyoponini: *Amblyopone australis* ERICHSON, *A. silvestrii* (WHEELER). Proceratiini: *Proceratium japonicum* SANTSCHI, *P. watasei* (WHEELER), *Discothyrea sauteri* FOREL, *D.* sp. Ectatommini: *Gnamptogenys costata* (EMERY), *Rhytidoponera purpurea* (EMERY), *R.* sp., Ponerini: *Brachyponera chinensis* (EMERY), *Cryptopone sauteri* (WHEELER), *Diacamma* sp., *Ectomomyrmex javanus* MAYR, *Hypoponera nippona* (SANTSCHI), *Leptogenys kitteli* MAYR, *L. confucii* FOREL, *Odontoponera transversa* (Fr. SMITH), *Ponera japonica* WHEELER, *P. scabra* WHEELER, *Trachymesopus pilosior* (WHEELER), *T. sharpi* FOREL, *Trapeziopela* sp. Odontomachini: *Odontomachus monticola* EMERY, *O.* sp., *Anochetus* sp.

The higher classification system of Formicidae was based on WHEELER and WHEELER (1985) as a guide line.

SEM observation. The spur structures were examined by SEM. The samples were cleaned by an ultrasonic-washer in the chloroform-methanol (2 : 1), dried in air, mounted on stubs and then sputtered with gold. To show the inner aspect of the cuticular structures, the samples were cut with a razor blade and the cellular material were digested with 10% KOH before the gold coating was applied.

Results

1. *Spur morphology*

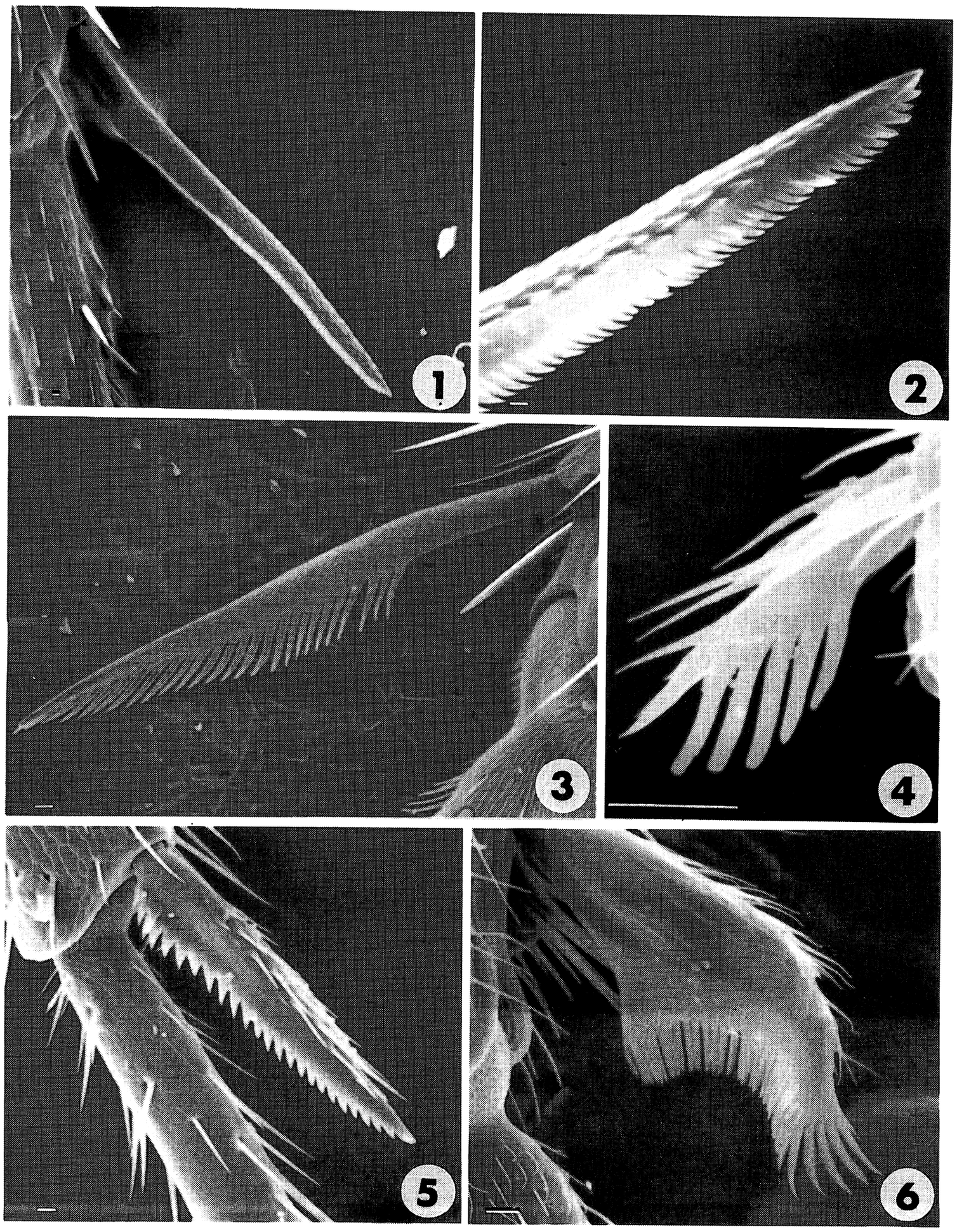
Five different types (S1-5) of the spur were morphologically recognized in Formicidae. Each of the types was characterized as follows;

S1. the spur, slender and straight, with a serrated edge (Figs. 1-2).

S2. the spur, triangle, bearing a row of fine teeth (Fig. 3).

S3. the spur, crescent, bearing a row of finger-like teeth (Fig. 4).
S4. the spur, triangle, bearing a row of teeth (Fig. 5).
S5. the spur, bent inward, bearing row of fine teeth (Fig. 6).

The S1 type spur was found only in Formicinae, while the S3, S4, and S5 type spurs were found in Leptanillinae, Dorylinae and Amblyoponini of Ponerinae, respectively. The other formicids examined here possessed the S2 type spur,



Figs. 1–6. Morphology of the hind-tibial spur. —— 1–2. *Camponotus japonicus* (Formicinae); 2, close-up of the apical part of the spur. —— 3. *Myrmecia gulosa* (Myrmeciinae). —— 4. *Leptanilla japonica* (Leptanillinae). —— 5. *Dorylus* sp. (Dorylinae). —— 6. *Amblyopone australis* (Ponerinae). (Scale bar = 10 μm)

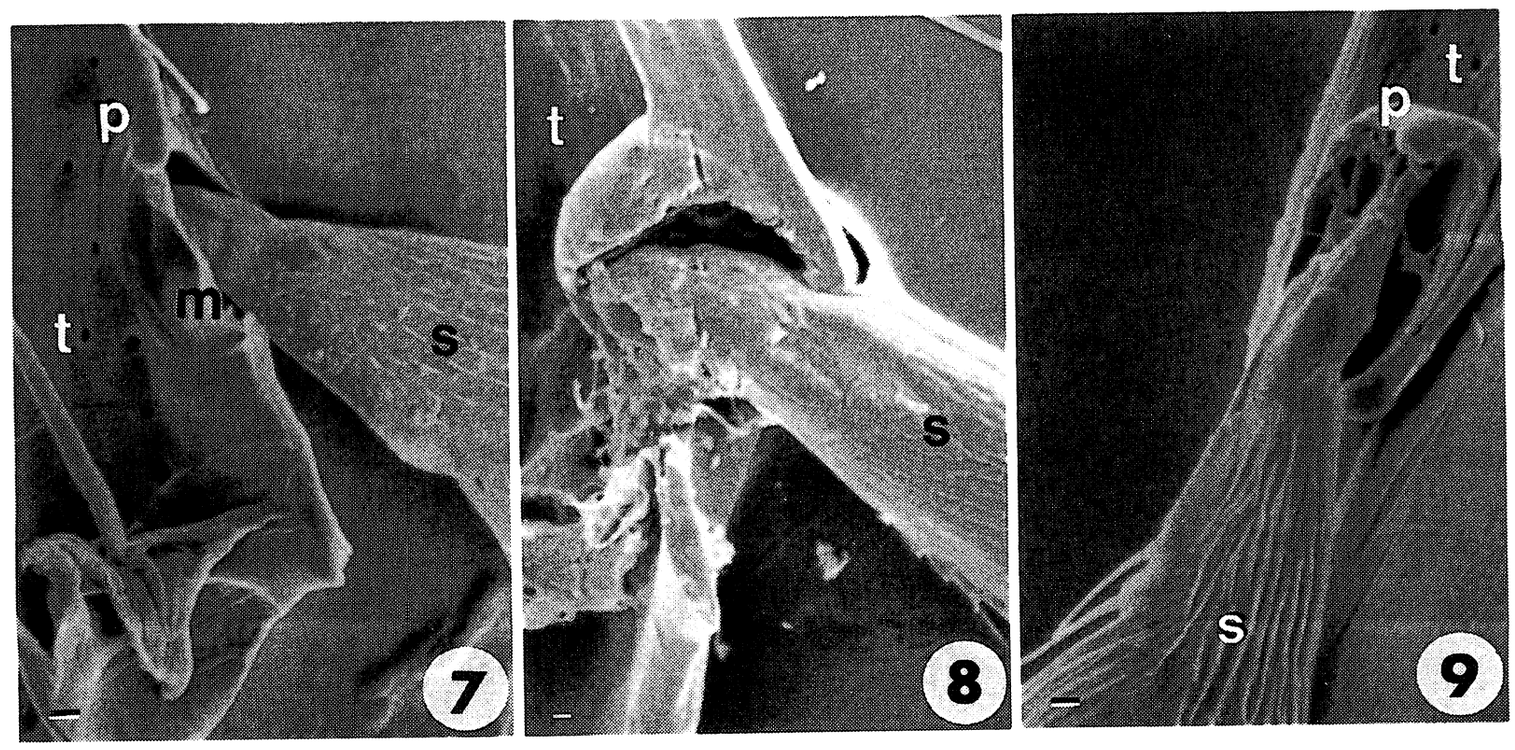
Table 2. Occurrence of different types of hind-tibial spur structures in subfamilies of Formicidae. The types are characterized in text.

Subfamily	Spur types	
	General morph. type	Articulation type
Formicinae	S1	A1
Dolichoderinae	S2	A2
Myrmeciinae	S2	A2
Pseudomyrmecinae	S2	A2
Dorylinae	S4	A2
Leptanillinae	S3	A2
Cerapachyinae	S2	A2
Ponerinae		
Amblyoponini	S5	A2
Proceratiini	S2	A2
Ponerini	S2	A2
Odontomachini	S2	A2
Ectatommini	S2	A2
Myrmicinae	S2	A2

though the loss of the spur has occurred in some Myrmicinae (*e.g.*, *Aphaenogaster*, *Crematogaster*, etc.) (Table 2).

2. *The spur articulation*

The spur is movable on an articulating membrane which forms the base of the socket in the distal end of the tibia (Fig. 7). Formicidae had two types (A1 and



Figs. 7–9. Internal aspect of the base of the hind-tibial spur. —— 7. *Leptogenys kitteli* (Ponerinae). —— 8. *Camponotus japonicus* (Formicinae), the socket membrane removed to show the basal part of the spur. —— 9. *Ectomomyrmex javanus* (Ponerinae), the socket membrane removed to show the basal part of the spur (m, membrane; p, process; s, spur; t, tibia). (Scale bar = 10 μm)

A2) of the spur articulation to the tibia. The first type had a thick base of the spur inserted in a socket without any special joints (A1) (Fig. 8). The second type had a thin base of spur inserted in a socket with a process forming a special support and articulation with the spur base (A2) (Figs. 7 and 9). The A1 type was found only in the subfamily Formicinae, whereas the A2 type was found in the other subfamilies so far examined (Table 2).

Discussion

This study revealed that the spur structures of the hind tibia in Formicidae contain sufficient variation to make use of them as phylogenetic characters. S1 type spurs (*i.e.*, the slender and straight spur with a serrated edge) were plesiomorphic (primitive) because this is the condition in most Aculeata (cf. SAINI & DHILLON, 1978). This conclusion may be supported by the earliest known fossil formicid, *Sphecomyrma freyi*. The photograph and illustration of *Sphecomyrma freyi* showed that the species had a slender and straight spur on the hind tibia, like that of Formicinae (cf. HÖLLDOBLER & WILSON, 1990). Several striking apomorphic types can be noted: S3 of Leptanillinae, S4 of Dorylinae and S5 of Amblyoponini. These types could be simply interpreted as independent derivations from S2 type, because the distribution of each type was restricted in certain taxa within the Formicidae, and because the spurs of these types (S3, S4, S5) and S2 type shared the same structure of the articulation to the tibia (A2 type). Since the spur set in the tibial socket with process, which was quite homologous with that on the fore leg (*i.e.*, the antennal clearner), has not been known in any other Aculeata (unpublished data), the A2 type of the spur articulation was regarded as apomorphic within the Formicidae.

Although Formicinae has been regarded as one of the more recently derived groups of Formicidae (WHEELER, 1922; 1928), HÖLLDOBLER and WILSON (1990) proposed a hypothesis that the subfamily diverged earlier in the formicid evolution mainly because only Formicinae lacked the pygidial gland. The fact that only Formicinae retained the plesiomorphic condition in the spur structure also supported this hypothesis.

S3, S4 and S5 type spurs have a possibility to define Leptanillinae, Dorylinae and Amblyoponini of Ponerinae, respectively, though more comprehensive data are needed to generalized the value of these morphological characters as ones applicable throughout the taxa. The leptanillines were initially treated as a tribe of Dorylinae, until WHEELER (1923) separated them as a subfamily Leptanillinae based on the larval morphology. However, because the adult leptanillines showed extreme morphological reduction that obscures their taxonomic status (BROWN 1954), it has been hoped for useful new characters to be found for adults. Unique morphology of the hind-tibial spur in the leptanillines could distinguish them from Dorylinae, as well as the other formicids.

To summarize, the hind-tibial spur of the family Formicidae showed wider diversity than BROTHERS (1975) indicated. The character transformations of the spur shape and the tibial-spur articulation indicated an early divergence of the subfamily Formicinae from the other existing subfamilies. In addition, the hind-tibial spur was useful in distinguishing the Leptanillinae, Dorylinae and Amblyoponini of Ponerinae so far as I examined. More survey of the spur structures among the Formicidae, particularly in the ponerine tribes, is on progress to elucidate the phylogeny of this family.

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